

## Chapter 2

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# Analysis of the relation between ungulate species richness in East Africa and climatic and remotely sensed productivity indices

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## Abstract

The aim of the study was to evaluate whether climatic or remotely sensed indices are a better predictor of ungulate species richness. Our hypothesis is that the remotely sensed index the normalized difference vegetation index (NDVI) integrates the influence of climatic and environmental factors, it should be a better predictor of species richness than climatic variables. The study was conducted in East Africa, which has high ungulate species diversity. Out of 95 ungulate species found in Africa, 55 are found within this sub-region. The vegetation is highly heterogeneous, with great variability in productivity that is influenced by the spatial and seasonal distribution of climatic variables, including precipitation and temperature. Species richness was regressed against each environmental variable, using linear, polynomial, logarithmic and exponential models. A test of the equality of two population regression coefficients was used to compare the models. The results show that the strongest correlates of species richness were rainfall and NDVI, with 69% and 55% of the variance explained. A unimodal pattern was exhibited for ungulate species richness with both rainfall and NDVI. The combination of rainfall and potential evapotranspiration (PET) best predicted the ungulate species richness. The climatic model was more predictive than NDVI ( $r^2$  of 0.76 vs. 0.55,  $t = 2.22$ ,  $P = 0.028$ ) in areas with a rainfall range between 200 and 1300 mm, and ( $r^2$  of 0.80 vs. 0.67,  $t = 1.32$ ,  $P = 0.10$ ) for the drier part of the rainfall gradient (<1000 mm) the difference was not significant. We concluded that NDVI was not a better predictor of species richness than integrated climatic indices. Several factors related to the reflectance of vegetation cover; soil-vegetation spectral mix and soil type /moisture limit the performance of NDVI in predicting both the primary productivity and species richness. Improvements in spectral, spatial and temporal resolutions, including information on surface radiation, ecosystem process variables (leaf area, leaf duration and primary productivity) and land cover characteristics should significantly improve the potential use of remotely sensed data in biodiversity studies.

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## 2.1 INTRODUCTION

Species diversity varies geographically and the factors permitting the coexistence of species are scale-dependent (Levin, 1992; Prins and Olff, 1998; Grace, 1999; Waide *et al.*, 1999). At sub-continental (areas  $> 10^6$  km<sup>2</sup>) or continental scale the productivity or energy flow through an ecosystem is considered a major determinant of species diversity (Currie, 1991; Rosenzweig and Abramsky, 1993; Wright *et al.*, 1993). However, the direct estimation of available energy is difficult at continental or sub-continental scales (Owen, 1988; Box *et al.*, 1989; Currie, 1991). Instead, diversity has been related to other indices that are related to energy flow, for example net aboveground primary productivity (NAPP) (Abramsky and Rosenzweig, 1984; Currie and Paquin, 1987; Owen, 1990; Currie, 1991; Wright *et al.*, 1993), as well as climatic parameters such as rainfall, potential and actual evapotranspiration, temperature and solar radiation (see reviews in Ricklefs and Schluter, 1993; Huston, 1994; Grace, 1999). The development of satellites for mapping and monitoring vegetation has introduced an alternative method for estimating NAPP, and it has been empirically established that the normalized difference vegetation index (NDVI) effectively measures photosynthetically active biomass (Justice *et al.*, 1985; Tucker *et al.*, 1985; Sellers, 1985; Box *et al.*, 1989; Prince, 1991a).

In the last decade NDVI has been related to the distribution of both plant and animal species diversity. Walker *et al.* (1992) correlated plant species richness to aggregated NDVI in California, while Jorgensen and Nohr (1996) related bird diversity to landscape diversity and biomass availability in the Sahel. Recently, Oindo and Skidmore (2002) and Baird (2001) related mammalian species richness to NDVI and its variability linked to seasonality and heterogeneity. A review of literature indicates that climatic and NDVI databases represent two different ways of approximating the spatial variability in NAPP. Climatic spatial databases are based on the interpolation of point observations from climatic stations. Using spatial extrapolation techniques, a few scattered climatic station samplings characterize NAPP over a large region (Walker *et al.*, 1992). NAPP is determined in part by other factors, such as soil fertility, soil physical and chemical characteristics, soil moisture, position in the terrain, and exposure to insolation (Bell, 1982; McNaughton, 1985; Belsky, 1989; Olff *et al.*, 2002). Thus, climatic databases may well provide a biased approximation of NAPP. On the other hand, NDVI images have been largely unexplored in biodiversity studies, though they cover large areas and can be frequently updated (Walker *et al.*, 1992; Jorgensen and Nohr, 1996). Various studies have shown that NDVI integrates the influence of climatic variables and other environmental factors (Cihlar *et al.*, 1991; Nicholson and Farrar, 1994; Richard and Pocard, 1998). This suggests that NDVI is a better predictor of NAPP and, compared with climatic indices, may reveal a stronger relationship with species diversity. Since NDVI integrates the influence of climatic variables and environmental factors such as soil fertility, it is hypothesized that NDVI would better predict species diversity than would climatic variables.

Thus the aim of the study is to evaluate whether climate-based or remote sensing-based productivity indices better predict species richness. Further, the distribution of species is discussed with respect to its implications for conservation. The term 'species diversity' refers to a number of species and the relative abundance of species, while 'species richness' refers to the total number (absolute value) of species inhabiting an area.

## 2.2 MATERIAL AND METHODS

### 2.2.1 Study area and data sets

The study area is East Africa - covering Kenya (569,260 km<sup>2</sup>), Tanzania (886,220 km<sup>2</sup>) and Uganda (207,950 km<sup>2</sup>). It is situated approximately between longitudes 12° South and 6° North and latitude 29° West and 42° East. The great diversity of ungulates is one of the most noticeable features of the East African region. Out of 95 ungulate species found in Africa, 55 are found within this sub-region.

The vegetation of East Africa is highly heterogeneous, with great variability in structure and productivity. The productivity is greatly influenced by the spatial and seasonal distribution of precipitation and temperature (Le Houerou and Hoste, 1977). Important vegetation types include forests, deciduous woodland, open and *Acacia* grassland, evergreen and thorn bushland, dwarf shrub grassland and sparsely vegetated grassland and shrubland in semi-desert areas.

The range of precipitation varies between and within the three countries (Brown and Cocheme, 1973; Pratt and Gwynne, 1977). Uganda has a range of 900 to 1300 mm, Tanzania 600 to 1300 mm, and Kenya 200 to 1300 mm. The three main rainfall patterns in the region are: year-long rainfall (around Lake Victoria), single season rainfall (northern Uganda, northwestern Kenya, most of Tanzania) and bimodal season rainfall (rest of Kenya).

### 2.2.2 Herbivore data

A total of 55 species belonging to two orders and six families were included in the analysis (Table 2.1). The orders Artiodactyla (Bovidae, Giraffidae, Hippopotamidae, Tragulidae and Suidae) and Perissodactyla (Equidae) were combined into one functional group – the ungulates. Digital data on large herbivore distribution at sub-continental level were acquired from the African Mammal Databank (Boitani *et al.*, 1999) and nomenclature was based on Wilson and Reeder (1993). The area hosts one critically endangered species (Hunter's hartebeest) and three endangered species (Ader's duiker, the Ruwenzori black-fronted duiker and Grevy's zebra). Several species are threatened, including the water chevrotain, the bay duiker, the yellow-backed duiker, Bate's pigmy antelope, the sitatunga, the bongo, and the black-fronted duiker. The rest of the species fall in the category of lower risk, but still depend on conservation programmes for their survival (IUCN, 1999).

*Ungulate diversity in relation to climatic and remotely sensed productivity indices*

**Table 2.1:** Listing of ungulate species included in the study. Nomenclature follows 'Mammals Species of the World' (Wilson and Reeder, 1993). Distribution data derived from Boitani *et al.* (1999).

Family	Common name	Species	Occurrence
Bovidae	Impala	<i>Aepyceros melampus</i> (Lichtenstein, 1812)	Kenya, Uganda and Tanzania
	Common hartebeest	<i>Alcelaphus buselaphus</i> (Pallas, 1766)	Kenya, Uganda and Tanzania
	Ader's duiker	<i>Cephalophus adersi</i> (Thomas, 1918)	Kenya, and Tanzania
	Bay duiker	<i>Cephalophus dorsalis</i> (Gray, 1846)	Uganda
	Harvey's red duiker	<i>Cephalophus harveyi</i> 120 (Thomas, 1893)	Kenya and Tanzania
	Blue duiker	<i>Cephalophus monticola</i> (Thunberg, 1789)	Kenya, Uganda and Tanzania
	Natal red duiker	<i>Cephalophus natalensis</i> (A. Smith, 1834)	Tanzania
	Black-fronted duiker	<i>Cephalophus nigrifrons</i> (Gray, 1871)	Kenya and Uganda
	Ruwenzori black-fronted duiker	<i>Cephalophus rubidus</i> (Thomas, 1901)	Uganda
	Red-flanked duiker	<i>Cephalophus rufilatus</i> (Gray, 1846)	Uganda
	Yellow-backed duiker	<i>Cephalophus silvicultor</i> (Afzelius, 1815)	Kenya and Uganda
	Abbott's duiker	<i>Cephalophus spadix</i> (True, 1890)	Tanzania
	Weyn's duiker	<i>Cephalophus weynsi</i> (Thomas, 1901)	Kenya, Uganda and Tanzania
	Blue wildebeest	<i>Connochaetes taurinus</i> (Burchell, 1823)	Kenya and Tanzania
	Hunter's antelope	<i>Damaliscus hunteri</i> (Sclater, 1889)	Kenya
	Topi, sassaby, tiang, korrigum	<i>Damaliscus lunatus</i> (Burchell, 1823)	Kenya, Uganda and Tanzania
	Grant's gazelle	<i>Gazella granti</i> (Brooke, 1872)	Kenya, Uganda and Tanzania
	Thomson's gazelle	<i>Gazella thomsonii</i> (Günther, 1884)	Kenya and Tanzania
	Roan antelope	<i>Hippotragus equinus</i> (Desmarest, 1804)	Kenya, Uganda and Tanzania
	Sable antelope	<i>Hippotragus niger</i> (Harris, 1838)	Kenya and Tanzania
	Common waterbuck	<i>Kobus ellipsiprymnus</i> (Ogilby, 1833)	Kenya, Uganda and Tanzania
	Kob	<i>Kobus kob</i> (Erxleben, 1777)	Uganda
	Puku	<i>Kobus vardonii</i> (Livingstone, 1857)	Tanzania
	Gerenuk	<i>Litocranius walleri</i> (Brooke, 1879)	Kenya and Tanzania
	Guentheri's dik-dik	<i>Madoqua guentheri</i> (Thomas, 1894)	Kenya and Uganda
	Kirki's damara dik-dik	<i>Madoqua kirki</i> (Günther, 1880)	Kenya and Tanzania
	Salt's dik-dik	<i>Madoqua saltiana</i> (Desmarest, 1816)	Kenya
	Bate's pigmy antelope	<i>Neotragus batesi</i> (de Winton, 1903)	Uganda
	Suni	<i>Neotragus moschatus</i> (Von Dueben, 1846)	Kenya and Tanzania
	Klipspringer	<i>Oreotragus oreotragus</i> (Zimmermann, 1783)	Kenya, Uganda and Tanzania
	Oryx or gemsbok	<i>Oryx gazella</i> (Linnaeus, 1758)	Kenya, Uganda and Tanzania
	Oribi	<i>Ourebia ourebi</i> (Zimmermann, 1783)	Kenya, Uganda and Tanzania
	Steinbok	<i>Raphicerus campestris</i> (Thunberg, 1811)	Kenya and Tanzania
	Sharpe's grysbok	<i>Raphicerus sharpei</i> (Thomas, 1897)	Tanzania
	Southern reedbuck	<i>Redunca arundinum</i> (Boddaert, 1785)	Tanzania
	Mountain reedbuck	<i>Redunca fulvorufula</i> (Afzelius, 1815)	Kenya, Uganda and Tanzania
	Bohor reedbuck	<i>Redunca redunca</i> (Pallas, 1767)	Kenya, Uganda and Tanzania
	Lichtenstein's hartebeest or konzi	<i>Sigmoceros lichtensteinii</i> (Peters, 1849)	Tanzania
	Common, grey or bush duiker	<i>Sylvicapra grimmia</i> (Linnaeus, 1758)	Kenya, Uganda and Tanzania
	African buffalo	<i>Syncerus caffer</i> (Spartman, 1779)	Kenya, Uganda and Tanzania
	Common eland	<i>Taurotragus oryx</i> (Pallas, 1766)	Kenya, Uganda and Tanzania
	Bongo	<i>Tragelaphus eurycerus</i> (Ogilby, 1837)	Kenya and Uganda
	Lesser kudu	<i>Tragelaphus imberbis</i> (Blyth, 1869)	Kenya, Uganda and Tanzania
	Bushbuck	<i>Tragelaphus scriptus</i> (Pallas, 1766 )	Kenya, Uganda and Tanzania
	Sitatunga	<i>Tragelaphus spekii</i> (Sclater, 1863)	Kenya, Uganda and Tanzania
	Greater kudu	<i>Tragelaphus strepsiceros</i> (Pallas, 1766)	Kenya, Uganda and Tanzania
Giraffidae	Giraffe	<i>Giraffa camelopardalis</i> (Linnaeus, 1758)	Kenya, Uganda and Tanzania
Hippopotamidae	Common hippopotamus	<i>Hippopotamus amphibius</i> (Linnaeus, 1758)	Kenya, Uganda and Tanzania
Suidae	Forest hog	<i>Hylochoerus meinertzhageni</i> (Thomas, 1904)	Kenya, Uganda and Tanzania
	Desert warthog	<i>Phacochoerus aethiopicus</i> (Pallas, 1766)	Kenya
	Common warthog	<i>Phacochoerus africanus</i> (Gmelin, 1788)	Kenya, Uganda and Tanzania
	Bushpig or Malagasy wild boar	<i>Potamochoerus larvatus</i> (F. Cuvier, 1822)	Kenya, Uganda and Tanzania
Tragulidae	Water chevrotain	<i>Hyemoschus aquaticus</i> (Ogilby, 1841)	Uganda
Equidae	Burchell's zebra	<i>Equus burchellii</i> (Gray, 1824)	Kenya, Uganda and Tanzania
	Grevy's zebra	<i>Equus grevyi</i> (Oustalet, 1882)	Kenya

### 2.2.3 Climatic and environmental variables

The climatic and environmental data were compiled from a number of sources. The climatic, soils and land cover data were generated from the ACTS database (ACTS, 1994). Solar radiation was computed from a digital elevation model (DEM) and algorithms as described in Kumar *et al.* (1997). The climatic database was developed based on data gathered by various organizations, such as local meteorological departments, the World Meteorological Organization (WMO), research organizations including CIMMYT, the Food and Agriculture Organization (FAO), the East Anglia Climate Research Unit and Texas A&M University. The climate grids were obtained by first fitting topographically dependent climate surfaces to point climate data, using procedures in the ANUSPLIN package (Hutchinson, 1991). The surfaces were then interpolated using elevations from the DEM, using the ANUCLIM package (McMahon *et al.*, 1995). Both elevation and climate data were subjected to comprehensive error detection and correction procedures based on ANUDEM and ANUSPLIN. Complete descriptions of the topographic and climate database for Africa are being prepared (Hutchinson *et al.*, in prep.).

The Advanced Very High Resolution Radiometer (AVHRR) on board the National Oceanic and Atmospheric Administration (NOAA) orbiting satellites collected the NDVI images used in the study. The AVHRR collects data over the entire globe twice daily, once during the daytime and once during the night-time. The vegetation index is derived as a function of the difference between the visible and near-infrared channels over the sum of the two channels. The sub-continental data set of 8 km resolution data was used to derive the aggregated NDVI maps. The NDVI data were downloaded from the African Data Dissemination Service (ADDS). The images covered the period 1982-1999. A total of 36 images were available for each year, based on the 10 days maximum value composite images. Detailed processing procedures and the calibration of the images are discussed in Los (1998). The downloaded images were calibrated for inter- and intra-sensor degradation and effects of El Chichcon and Mt Pinatubo volcanic events.

### 2.2.4 Derivation of spatial data sets

The resampling of the distribution of ungulate species richness to match the environmental variables was realised at 1.5° by 1.5° or 167 km by 167 km quadrat (refer to methodology in Schall and Pianka, 1978; Owen, 1990; Currie, 1991; Anderson and Marcus, 1993). The number of ungulate species occurring in each quadrat was established by overlaying 55 species maps with a regional 1.5° by 1.5° quadrat map. The total number of species occurring in each quadrat was taken as the species richness for that quadrat. The values for rainfall, potential evapotranspiration (PET), temperature, solar radiation, NDVI and elevation variables were determined using the average value for each quadrat.

### *2.2.5 Statistical analysis*

The relation between species richness and productivity was determined by examining bivariate plots of species richness and each of the explanatory variables. Species richness was regressed against each environmental variable, using linear, polynomial, logarithmic and exponential models. The fitting of higher polynomial order models was used if they provided a statistical improvement in fit. The best fitting model was selected based on the *F*-test (Zar, 1996). A test of the equality of two population regression coefficients (Zar, 1996) was used to compare the pair of models. Tests for independence of the residual (Durbin-Watson test) and normality (Kolmogorov-Smirnov test) were conducted for each model.

In the next stage of the analysis the most important climatic variables for explaining the variation in ungulate species richness were investigated. Using stepwise regression models the probability of each variable entering, and staying in, the model was set at  $P = 0.05$ . Finally a comparison between the integrated climatic model and the NDVI model was assessed. The statistical analyses were performed in Systat 7.0.1 (SPSS Inc., 1997).

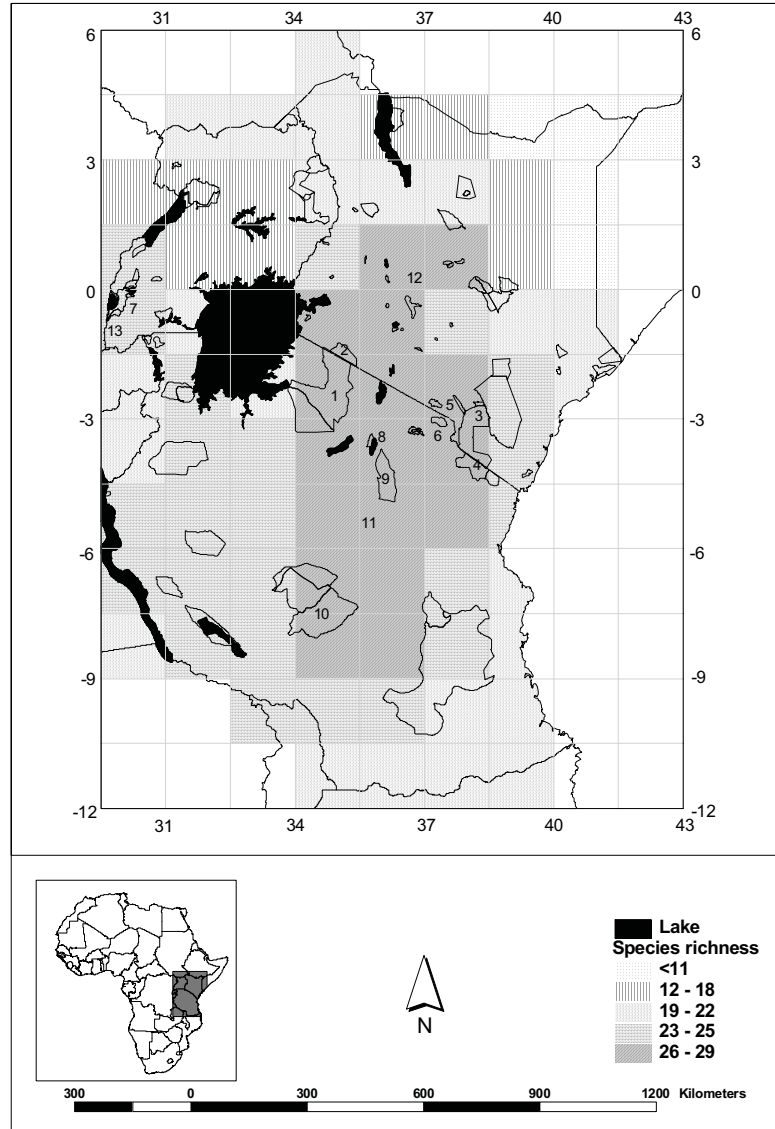
## **2.3 RESULTS**

### *2.3.1 General ungulate species richness patterns*

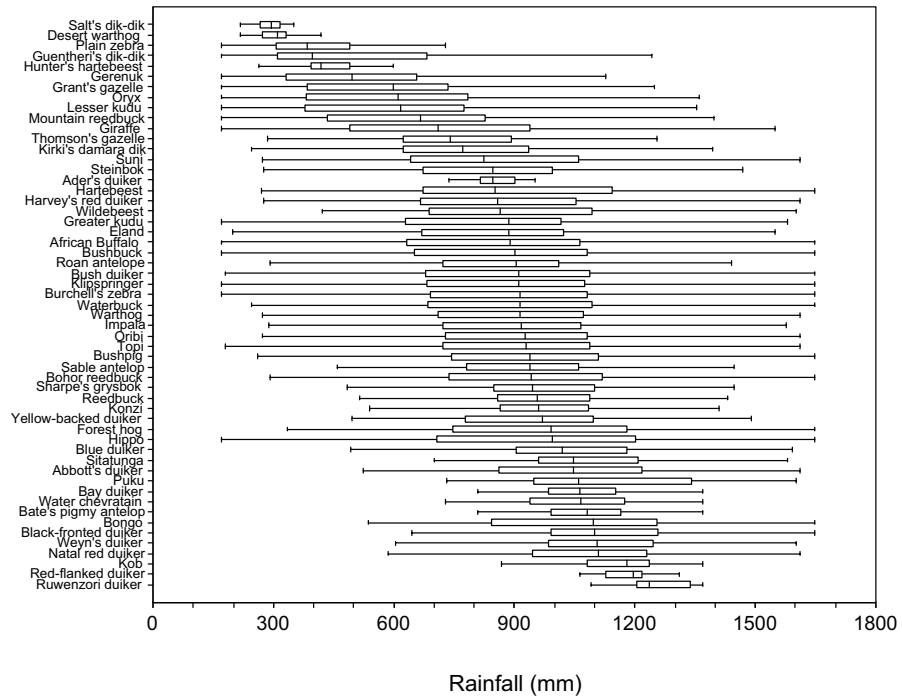
Table 2.1 reveals that at country level Tanzania and Kenya host a higher number of ungulate species than Uganda. Figure 2.1 shows the spatial distribution of ungulate species richness in East Africa. A pronounced latitudinal gradient is apparent, with maximum richness between 0° North and 9° South. Longitudinal patterns were not strongly evident, though species richness was higher between longitudes 34° and 38° East. The highest species richness occurred mainly in the *Acacia* grasslands and grassy shrublands of northern and central Tanzania and southwestern Kenya, with most of the surrounding areas having medium species richness. Low species richness occurred mainly in the extreme arid environments of northern Kenya and northern Uganda. The distribution of individual species in relation to rainfall gradient is shown in Figure 2.2.

### *2.3.2 Species richness-productivity relationship*

Figure 2.3 shows the relation between species richness and four NAPP indices. The relation between species richness and NDVI and rainfall reveals a unimodal or a hump-shaped pattern (Figure 2.3a and Figure 2.3b). A second-order polynomial regression best describes this relationship, while a third-order model did not significantly improve the fit ( $R^2$  of 0.55 vs. 0.56;  $F = 0.41$  and  $P = 0.66$ ). A third-order polynomial best describes the pattern ( $R^2$  of 0.69). The relationship between species richness and temperature and PET was revealed to be linear (Figs 2.3c and d). There was no significant relation between species richness and total solar radiation.

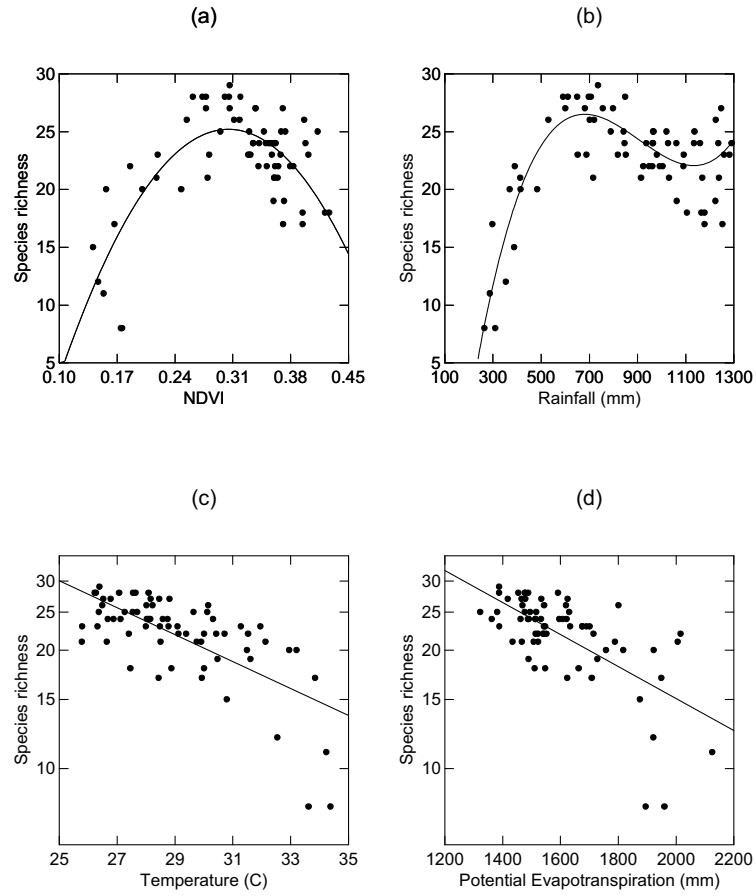


**Figure 2.1:** Distribution of number of ungulate species per grid cell of 1.5° by 1.5° in East Africa. The map is based on the overlay of 55 species maps. Protected and adjacent sites that have high species richness include <sup>1</sup>Serengeti-<sup>2</sup>Masai Mara ecosystem, <sup>3</sup>Tsavo-<sup>4</sup>Mkomazi ecosystem, <sup>5</sup>Amboseli-<sup>6</sup>Loliondo ecosystem, <sup>7</sup>Queen Elizabeth National Park and surrounding areas, <sup>8</sup>Manyara-<sup>9</sup>Tarangire ecosystem and <sup>10</sup>Ruaha-Rungwa ecosystem. Non-protected areas that exhibit high species richness include <sup>11</sup>parts of central Tanzania, <sup>12</sup>Laikipia-Samburu and <sup>13</sup>southwestern Uganda.



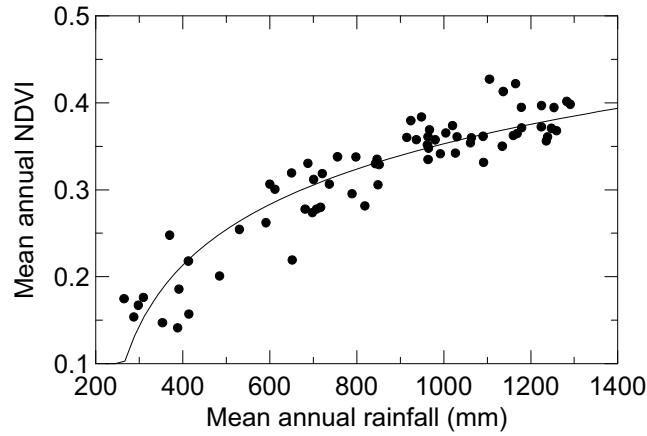
**Figure 2.2:** A boxplot showing the relation between species distribution and average rainfall within East Africa. The central vertical line in each box represents the median and the bars represent 1.5 of the inter-quartile range above the third quartile or below the first quartile.





**Figure 2.3:** Relationship between ungulate species richness and mean annual values of four variables related to primary productivity in East Africa. Data points refer to areas of  $1.5^{\circ} \times 1.5^{\circ}$  (refer to Table 2.2 for detailed equations for each relationship).

The relationship between rainfall and NDVI is shown in Figure 2.4. It reveals that the NDVI value levels off at higher rainfall values, and possibly reaches an asymptote somewhere beyond 1400 mm of rainfall ( $\text{NDVI} = -0.7725 + 0.1613\text{Ln}(P)$ ,  $P < 0.0001$ ,  $r^2 = 0.87$ ,  $n = 69$ ).



**Figure 2.4:** Relationship between mean annual precipitation and mean annual NDVI in East Africa; the relationships level off at higher rainfall values of about 1000 mm.

Table 2.2 summarizes the results of the statistical analysis of the relation between species richness and four environmental factors related to NAPP. The analysis was run for the whole range of rainfall (200 – 1300 mm), as well as for a shorter rainfall range (200 – 1000 mm) where rainfall and NDVI were linearly related. The strongest correlates of species richness were rainfall and NDVI, with 69% and 55% of the variance in richness explained. The variance explained increased towards 80% and 67%, respectively, when considering the drier part of the rainfall gradient.

We next compared the best-fit climatic model (including a number of climatic variables) with the best-fit remotely sensed model (Table 2.3). Rainfall and PET explained a significantly higher proportion of the variance in species composition than remotely sensed data did. This conclusion was valid for the whole range of rainfall (200 – 1300 mm;  $t = 2.22$ ,  $P = 0.028$ ) but not significant for the drier end of the rainfall gradient (200 – 1000 mm;  $t = 1.32$ ;  $P = 0.01$ ).

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**Table 2.2:** Regression equations describing the best fitting model of polynomial (fourth order), exponential and logarithmic functions fitted between species richness and four factors related to NAPP.

Rainfall range (mm)	Factors	Model	$r^2$	$n$
200 - 1300	Precipitation	$-34.01 + 2.22*10^{-1}x - 2.61*10^{-4}x^2 + 1*10^{-7}x^3$	.69*	69
	Temperature	$61.77 - 1.3568x$	.47*	
	Potential evapotranspiration	$49.34 - 0.0167x$	.44*	
	NDVI	$-22.22 + 311.26x - 510.71x^2$	.55*	
<1000	Precipitation	$-13.71 + 1.09*10^{-1}x - 7.5*10^{-5}x^2$	.77*	44
	Temperature	$74.19 - 1.7459x$	.66*	
	Potential evapotranspiration	$55.89 - 0.0201x$	.56*	
	NDVI	$-27.75 + 357.35x - 595.99x^2$	.67*	
1000 - 1300	Precipitation		ns	25
	Temperature	$41.18 - 0.79x$	.21***	
	Potential evapotranspiration	$55.40 - 0.02x$	.45**	
	NDVI		ns	

ns = not significant; \* =  $P < 0.0001$ ; \*\* =  $P < 0.001$ ; \*\*\* =  $P < 0.05$

**Table 2.3:** Regression equations describing the best fitting model between species richness and combined climatic variables, respectively remotely sensed variables, for two ranges of rainfall.

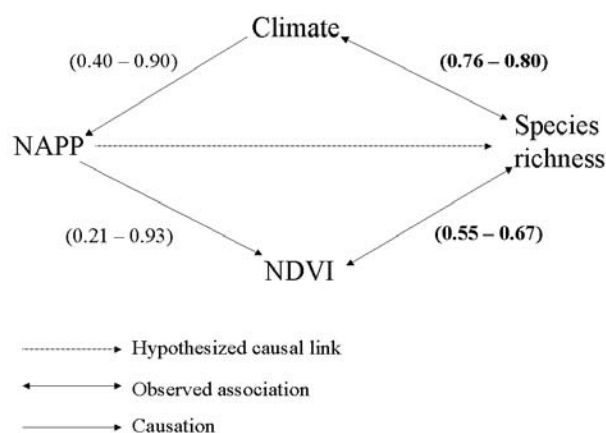
Rainfall range (mm)	Factors	Model	$r^2$	$n$
200 - 1300	Climatic	$-1.24 + 1.81*10^{-1}P - 22.26*10^{-4}P^2 + 8*10^{-8}P^3 - 1.17*10^{-2}PET$	.76	69
	Remotely sensed	$-22.22 + 311.26NDVI - 510.71NDVI^2$	.55	
200 - 1000	Climatic	$6.44 + 9.00*10^{-2}P - 7.57*10^{-3}P^2 - 6.33*10^{-5}PET$	.80	44
	Remotely sensed	$-27.75 + 357.35NDVI - 595.99NDVI^2$	.67	

All models were significant at  $P < 0.0001$ . P = Precipitation; PET = Potential evapotranspiration; and NDVI = Normalized difference vegetation index.

## 2.4. DISCUSSION

### 2.4.1 Predictor of ungulate species diversity – climatic indices versus remotely sensed NDVI

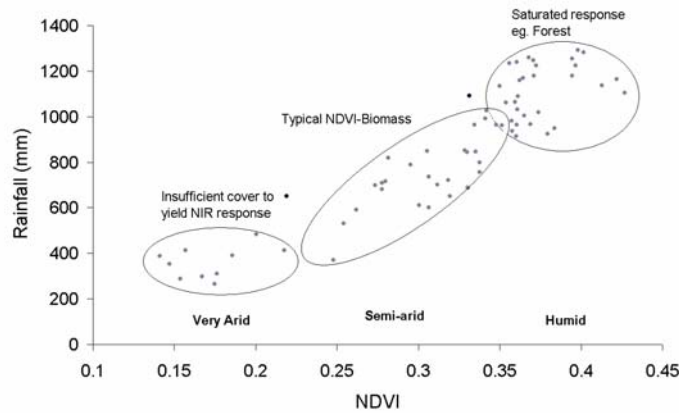
The results from this study reveal that the remotely sensed index was not a better predictor of species richness than integrated climatic indices. This is contrary to our initial expectation and contradicts established literature (Nicholson *et al.*, 1990; Walker *et al.*, 1992; Stoms and Estes, 1993; Los, 1998b). The climatic model was more predictive than NDVI in areas with a rainfall range between 200 and 1300 mm; for the drier part of the rainfall gradient (<1000 mm) the difference was not significant. The difference in variance explained by the two models was investigated by reviewing the literature that related NDVI and climatic variables to NAPP. Figure 2.5 summarizes the conceptual model of primary relationships controlling species richness.



**Figure 2.5:** Scheme of the relation between species richness, NAPP, climate and NDVI. NAPP is hypothesized to have a causal link with species diversity. We expected that NDVI would be a better predictor of species diversity. This was not the case; climatic factors proved to be superior predictors. Values in brackets indicate range of  $r^2$  values reported in this study (bold), respectively range of values reported in other studies (regular).

The relationship between rainfall and productivity shows that the coefficient of determination ranged between 0.40 and 0.90. In sub-Sahara Africa productivity generally relates well to average rainfall (Le Houerou and Hoste, 1977; Deshmukh, 1984; McNaughton, 1985; van Wijngaarden, 1985; Boutton *et al.*, 1988; Box *et al.*, 1989). However, the problems associated with rainfall-productivity models are linked to sampling a few points only and interpolating the data over large areas, as well as failure to incorporate all factors related to NAPP – soil and plant characteristics and resource regulators (Le

Houderou and Hoste, 1977; Box, 1978; Box *et al.*, 1989). The published information on the relationship between NDVI and productivity varies, with the coefficient of determination ranging between 0.21 and 0.93 (refer to Figure 2.5; McNaughton, 1976; Boutton and Tieszen, 1983; Tucker *et al.*, 1985; Diallo *et al.*, 1991; Prince, 1991b; Wylie *et al.*, 1991; Hobbs, 1995). The variation between rainfall and NDVI can be related to the reflectance property of the vegetation cover, as illustrated in the schematic diagram shown in Figure 2.6.



**Figure 2.6:** Relationship between rainfall and NDVI, which indicates poor correlation in the very arid and humid areas; a strong relation is observed in the semi-arid areas (refer to the text for detailed description).

The problems associated with the vegetation index in arid areas are mainly due to soil-vegetation spectral mixing (Heute and Tucker, 1991). In poorly vegetated areas there is insufficient cover to yield a reflectance response near infrared (NIR). In the semi-arid areas the relation is much stronger, with NDVI being linearly correlated with productivity. In the humid areas above a certain threshold (in this study 1000 mm), the NDVI is not sensitive to rainfall variations (Sellers, 1985; Box *et al.*, 1989; Nicholson *et al.*, 1990). In addition to vegetation cover other factors such as soils and atmospheric conditions can minimize the accuracy of predicting NAPP based on NDVI. It has been observed in partially vegetated areas (40–75% green cover) that soil darkening due to moisture or soil type can increase the NDVI by 25% (Heute and Tucker, 1991; Nicholson and Farrar, 1994). Water vapour and aerosol, however, have been reported to reduce the integrated NDVI by about 30 to 60% (Justice *et al.*, 1991). The further improvements in spectral, spatial and temporal resolutions to be introduced in the new satellite sensors, including information on surface radiation, ecosystem variables (leaf area, leaf duration and primary productivity) and land cover

characteristics, should significantly improve the potential use of remotely sensed data in biodiversity studies.

This study has established that climatic model was more predictive than NDVI in areas with a rainfall range between 200 and 1300 mm; for the drier part of the rainfall gradient (<1000 mm) the difference was not significant. The factors discussed in this study indicate the limitations of NDVI in predicting NAPP and could have contributed significantly to the fact that the NDVI model did not perform better than the climatic model in predicting species richness. This observation is supported by a number of studies relating species richness to NDVI. Most of these studies have reported lower correlations between plant or mammalian species richness and NDVI (see Walker *et al.*, 1992; Jorgensen and Nohr, 1996; Oindo *et al.*, 2000; Baird, 2001; Oindo and Skidmore, 2002; this study) than those studies using climatic variables as proxy for productivity (refer to Abramsky and Rosenzweig, 1984; Owen, 1988; Owen, 1990; Currie, 1991; Prins and Olff, 1998; Waide *et al.*, 1999; Balmford *et al.*, 2001; Olff *et al.*, 2002).

#### *2.4.2 Ungulate species diversity pattern and its implication for conservation*

The species richness in East Africa is best described as unimodal in pattern (refer to Figure 2.3b). The strongest single factor that best predicated ungulate species richness was rainfall. Contrary to expectations that high productive areas would have high species richness (energy limitation theory – see Wright, 1983), ungulates were highest at the intermediate productivity level. The pattern is consistent with studies on variations in richness (plants and animals) as functions of productivity that show species richness reaches its maximum at intermediate productivity levels (see Grime, 1973; Huston, 1980; Tilman, 1982; Abramsky and Rosenzweig, 1984; Al-Mufti *et al.*, 1984; Owen, 1988; Rosenzweig and Abramsky, 1993; Prins and Olff, 1998; Huston, 1999; Balmford *et al.*, 2001; Olff *et al.*, 2002). The hump-shaped curve of the species richness-productivity relationship appears to be composed of at least two phases: the positive (Kenya) and negative slopes (Tanzania and Uganda) that make up the two sides of the hump-shaped curve, with maximum species richness occurring in both Kenya and Tanzania.

A number of studies have shown that ungulate species diversity varies across gradients of plant abundance and quality (Western, 1975; Coe *et al.*, 1976; Bell, 1982; East, 1984; McNaughton, 1985; Prins and Olff, 1998; Olff *et al.*, 2002). Olff *et al.* (2002) further suggested that herbivore species must encounter plants of both sufficient abundance and quality to persist, and therefore may be constrained to persist only under certain conditions of plant-available moisture and nutrients. The highest herbivore density is thus expected in locations that are neither so wet and/or infertile that average plant quality would be too low to sustain smaller herbivores, nor so dry and/or infertile that plant productivity would be insufficient to sustain larger herbivores. The dry and infertile habitats have low population abundance – raising extinction rates, which may limit species diversity (Rosenzweig and Abramsky, 1993). While the low biomass of herbivore communities in moist savannas reflects the limitation imposed by vegetation quality rather than quantity (Bell, 1982; Olff *et al.*, 2002), the isolation of the population of *Cephalophus* and *Sylvicapra* (mainly the duikers) in the forest environment over time may also have segregated the group from other

ungulate species, preventing frequent mixing (Sinclair, 1983). Abrams (1995) argued that such taxonomic groups are likely to have their highest diversity in the types of environment where they have spent most of their evolutionary history.

The implication of these patterns is that both the savanna and forest ecosystems have a high diversity of ungulate species. Balmford *et al.* (2001) found high correlation between species richness and population density in Africa. These findings have been supported by local studies which have shown that increased encroachment and fragmentation of wildlife habitat through uncontrolled expansion of agriculture (Newmark, 1996; Ottichilo, 2000; Homewood *et al.*, 2001), deforestation (Chapman and Lambert, 2000), illegal killings (Caro *et al.*, 1998; McRae, 1998; Mduma *et al.*, 1998) and the introduction of artificial water points (de Leeuw *et al.*, 2001) have negatively affected wildlife diversity in East Africa. Most of these changes are occurring in the areas of high species diversity. The overall effects may be reflected in the current status of the ungulate species, where out of the 55 species studied here, one is critically endangered, three are threatened, seven are near threatened and the rest depend on the conservation status where they are located. Immediate action is needed to further manage and conserve areas of high species richness, and the models developed in this study could be used as a first step in mapping potential conservation areas that need attention.

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